

GLOBAL DYNAMICS OF A LOTKA–VOLTERRA MODEL WITH TWO PREDATORS COMPETING FOR ONE PREY

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ABSTRACT. In this paper we study the global dynamics of 3-dimensional predator-prey Lotka–Volterra systems, which describes two predators competing for food or shared one resource. From theoretical analysis on all parameters of this system, we show that if the resource for prey is limited, then there exist some values of parameters such that two predators and one prey coexist and their population are asymptotic to steady states. Otherwise, at least one of two predator species is extinct. On the other hand, if the resource for prey is unlimited, then there are the complete classification of parameters values such that the system has two possible global dynamics. Either every solution of the system is asymptotic to a closed orbit, or to the equilibrium in the invariant coordinate plane, or every solution of the system is a periodic orbit except the equilibrium in the positive octant of \mathbb{R}^3 . This implies that the principle of competitive exclusion holds for some values of parameters of the Lotka–Volterra system, and it does not hold for the other values of parameters of the Lotka–Volterra system. Hence, there are only two coexistence styles for all three species: periodic oscillation or steady states, which depends on the resource for prey. The results have an importance biological implication in pest control.

1. INTRODUCTION

The study of the dynamics of predator–prey systems was originated in the works of Lotka [17] and Volterra [25] who considered a model for one predator and one single prey in a constant and uniform environment, known now as the *standard Lotka–Volterra model*. In this model the populations of predator and prey permanently oscillate for almost all positive initial conditions. In the same work, Volterra also argued that the coexistence of two or more predators competing for fewer prey resources is impossible, this claim was called the *principle of competitive exclusion* (see [1], [7], [19]).

Hsu and Hubbell in [9] studied 4-dimensional Lotka–Volterra models with two competing predators sharing two prey species under the assumption that prey species were capable of self-reproduction and regenerated logistically in the absence of consumption, and obtained some conditions under which the competing predators survive or die out. Their results revealed that the principle of competitive exclusion was true for some of parameters values in the Lotka–Volterra model with two competing predators sharing two prey species. Note that the predator functional response to the prey density is linear in the Lotka–Volterra model. When the predator functional response to the prey density is nonlinear, the principle of

1991 *Mathematics Subject Classification.* 37N25, 34C12, 34C28, 37G20.

Key words and phrases. Predator–prey, Lotka–Volterra model, global dynamics, extinction, coexistence.

competitive exclusion was re-examined by Koch in [13] via numerical simulation, which showed that the coexistence of two predators competing for a single prey species was in fact possible when the predator functional response to the prey density was assumed according to the Michaelis–Menten kinetics, and such coexistence occurred along what appeared to be a periodic orbit in the positive octant of \mathbb{R}^3 rather than an equilibrium.

Hsu, Hubbell and Waltman in [10, 11] studied the competition problem of the two predators for a single prey model. By combining theoretical analysis with numerical simulations, they obtained the parameter range of the validity of the principle of competitive exclusion, and provided a wide range of parameter values for the coexistence of two predators numerically. Following these numerical observations, there have been several important theoretical developments in justifying the coexistence for two predators competing for a single prey species model with nonlinear functional responses. In which bifurcation techniques were applied to the model for obtaining a stable periodic orbit in the positive octant of \mathbb{R}^3 . This stable periodic orbit bifurcates from a 2-dimensional predator–prey limit cycle in the plane, which implies the coexistence of two competing predators (see [3], [12], [22], [23] and their references therein). Muratori and Rinaldi in [20] first considered the problem by singular perturbation arguments. Using dynamical systems techniques and the geometric singular perturbation theory, Liu, Xiao and Yi in [16] gave precise conditions which guarantee the coexistence of two predators for the model via rigorous analysis.

It is well known that resource competition is common in nature and society. Global dynamics of the resource competitive model is important to understand the mechanism of natural selection: the principle of competitive exclusion and the coexistence of competing species. There have been some excellent works such as [15], [26] and so on.

The aim of this paper is to study the global dynamics of 3-dimensional Lotka–Volterra models with two predators competing for a single prey species in a constant and uniform environment. It is assumed that the two predator species compete purely exploitatively with no interference between rivals, the growth rate of the prey species is logistic or linear in the absence of predation, respectively, and the predator’s functional response is linear. Then the model is a system of ordinary differential equations of the form

$$(1) \quad \begin{aligned} \frac{dS(t)}{dt} &= S(t) \left(r_3 - \frac{1}{K} S(t) - b_1 x_1(t) - b_2 x_2(t) \right), \\ \frac{dx_1(t)}{dt} &= x_1(t) (-r_1 + a_1 S(t)), \\ \frac{dx_2(t)}{dt} &= x_2(t) (-r_2 + a_2 S(t)), \end{aligned}$$

where $x_i(t)$ for $i = 1, 2$ represents the population density of the i -th predator at time t , $S(t)$ represents the population density of the prey at time t , $r_3 > 0$ is the intrinsic rate of growth of the prey, $K > 0$ is the carrying capacity of the prey, which describes the richness of resources for prey. If $K = \infty$, then prey can increase unlimited, which implies that the growth rate of the prey species is linear in the absence of predation; $b_i > 0$ is the effect of the i -th predation on the prey, $r_i > 0$ is the natural death rate of the i -th predator in the absence of prey, a_i is the efficiency

and propagation rate of the i -th predator in the presence of prey. It is clear that $x_i(t) \geq 0$ and $S(t) \geq 0$. Hence, system (1) is considered only in the closed positive octant \mathbb{R}_+^3 , of course here $\mathbb{R}_+ = [0, \infty)$. For simplicity, we denote the open positive octant by $\text{Int}(\mathbb{R}_+^3)$.

We completely characterize the qualitative behavior of system (1) in two cases: the limited resource for prey (i.e. K is bounded) and the unlimited resource for prey (i.e. $K = \infty$). It is shown that as K is bounded, there exist some values of parameters of system (1) such that two predators and one prey coexist and their population are asymptotic to steady states. Otherwise one of two predators species is extinct. On the other hand, if $K = \infty$, then there are only two possible global dynamics for the system. Either the system has a global attractor which is a boundary equilibrium, or every solution of the system is a periodic orbit in the positive octant of \mathbb{R}^3 . These results imply that the principle of competitive exclusion hold for some values of parameters of the Lotka-Volterra system, and it does not hold for the other values of parameters of the Lotka-Volterra system. And there are only two coexistence styles for all three species of system (1): periodic oscillation or steady states, which depends on the resource for prey.

This paper is organized as follows. In section 2 we study the global dynamics of the two predators-one prey system as K is a bounded parameter. In section 3 we study the global dynamics of the two predators-one prey system when $K = +\infty$. The paper ends with a brief discussion.

2. GLOBAL DYNAMICS OF SYSTEM (1) WITH LIMITED RESOURCE FOR PREY

In this section we consider system (1) with the bounded K in \mathbb{R}_+^3 . We first study the existence and topological classification of finite equilibria and equilibria at infinity for system (1), then we study the global dynamics of this system.

2.1. The existence and topological classification of equilibria. It is clear that system (1) has an equilibrium at the origin $O(0, 0, 0)$, and an equilibrium at the point $E_0(r_3K, 0, 0)$ for all the values of the parameters. Except the two boundary equilibria, system (1) may have other boundary equilibria and the positive equilibria in \mathbb{R}_+^3 for some values of parameters. Doing easy algebra calculations we obtain the following result.

Proposition 1. *The following statements hold.*

- (i) *System (1) has a boundary equilibrium $E_1\left(\frac{r_1}{a_1}, \frac{1}{b_1}(r_3K - \frac{r_1}{a_1}), 0\right)$ in \mathbb{R}_+^3 except the boundary equilibria O and E_0 if $r_3K > \frac{r_1}{a_1}$; and system (1) has a boundary equilibrium $E_2\left(\frac{r_2}{a_2}, 0, \frac{1}{b_2}(r_3K - \frac{r_2}{a_2})\right)$ in \mathbb{R}_+^3 except the boundary equilibria O and E_0 if $r_3K > \frac{r_2}{a_2}$.*
- (ii) *System (1) has positive equilibria $E_+(S, x_1, x_2)$ in $\text{Int}(\mathbb{R}_+^3)$ if and only if $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ and $r_3K > \frac{r_1}{a_1}$. And if system (1) has a positive equilibria in $\text{Int}(\mathbb{R}_+^3)$, then system (1) has infinitely many positive equilibria $E_+(S, x_1, x_2)$ in $\text{Int}(\mathbb{R}_+^3)$, which fill up a segment L with endpoints at boundary equilibria E_1 and E_2 , respectively in $\text{Int}(\mathbb{R}_+^3)$, where*

$$L = \{(S, x_1, x_2) : S = \frac{r_1}{a_1}, b_1x_1 + b_2x_2 = r_3K - \frac{r_1}{a_1}, x_1 \geq 0, x_2 \geq 0\}.$$

We now study the local phase portraits of the boundary equilibria and positive equilibria. Since the Jacobian matrix $J(S, x_1, x_2)$ of system (1) at an equilibrium (S, x_1, x_2) is

$$J(S, x_1, x_2) = \begin{pmatrix} r_3 - \frac{2}{K}S - b_1x_1 - b_2x_2 & -b_1S & -b_2S \\ a_1x_1 & -r_1 + a_1S & 0 \\ a_2x_2 & 0 & -r_2 + a_2S \end{pmatrix},$$

we obtain the following local phase portraits for the equilibria after some computations and the applications of standard results.

Proposition 2. *The following statements hold.*

- (i) $O(0, 0, 0)$ is a saddle with a 2-dimensional stable manifold and an 1-dimensional unstable manifold for all parameters.
- (ii) $E_0(r_3K, 0, 0)$ has the following local phase portraits depending on the values of the parameters.
 - (ii.a) E_0 is a stable node if $r_3K < \min\{\frac{r_1}{a_1}, \frac{r_2}{a_2}\}$;
 - (ii.b) E_0 is saddle with a 2-dimensional stable manifold and an 1-dimensional unstable manifold if $\min\{\frac{r_1}{a_1}, \frac{r_2}{a_2}\} < r_3K < \max\{\frac{r_1}{a_1}, \frac{r_2}{a_2}\}$;
 - (ii.c) E_0 is saddle with a 1-dimensional stable manifold and a 2-dimensional unstable manifold if $\max\{\frac{r_1}{a_1}, \frac{r_2}{a_2}\} < r_3K$;
 - (ii.d) E_0 is degenerated equilibrium if either $r_3K = \frac{r_1}{a_1}$ or $r_3K = \frac{r_2}{a_2}$.
- (iii) $E_1(\frac{r_1}{a_1}, \frac{1}{b_1}(r_3K - \frac{r_1}{a_1}), 0)$ has the following local phase portraits depending on the values of the parameters.
 - (iii.a) E_1 is a stable node if $\frac{r_1}{a_1} < r_3K \leq \frac{r_1 + \sqrt{r_1^2 + r_1r_3}}{2a_1}$ and $\frac{r_1}{a_1} < \frac{r_2}{a_2}$;
 - (iii.b) E_1 is saddle with a 2-dimensional stable manifold and an 1-dimensional unstable manifold if $\frac{r_1}{a_1} < r_3K \leq \frac{r_1 + \sqrt{r_1^2 + r_1r_3}}{2a_1}$ and $\frac{r_1}{a_1} > \frac{r_2}{a_2}$;
 - (iii.c) E_1 is stable focus if $r_3K > \frac{r_1 + \sqrt{r_1^2 + r_1r_3}}{2a_1}$ and $\frac{r_1}{a_1} < \frac{r_2}{a_2}$;
 - (iii.d) E_1 is a saddle-focus with a 2-dimensional stable manifold and an 1-dimensional unstable manifold if $r_3K > \frac{r_1 + \sqrt{r_1^2 + r_1r_3}}{2a_1}$ and $\frac{r_1}{a_1} > \frac{r_2}{a_2}$;
 - (iii.e) E_1 is a degenerated equilibrium if $\frac{r_1}{a_1} < r_3K$ and $\frac{r_1}{a_1} = \frac{r_2}{a_2}$.
- (iv) $E_2(\frac{r_2}{a_2}, 0, \frac{1}{b_2}(r_3K - \frac{r_2}{a_2}))$ has the following local phase portraits depending on the values of the parameters.
 - (iv.a) E_2 is a stable node if $\frac{r_2}{a_2} < r_3K \leq \frac{r_2 + \sqrt{r_2^2 + r_2r_3}}{2a_2}$ and $\frac{r_1}{a_1} > \frac{r_2}{a_2}$;
 - (iv.b) E_2 is saddle with a 2-dimensional stable manifold and an 1-dimensional unstable manifold if $\frac{r_2}{a_2} < r_3K \leq \frac{r_2 + \sqrt{r_2^2 + r_2r_3}}{2a_2}$ and $\frac{r_1}{a_1} < \frac{r_2}{a_2}$;
 - (iv.c) E_2 is stable focus if $r_3K > \frac{r_2 + \sqrt{r_2^2 + r_2r_3}}{2a_2}$ and $\frac{r_1}{a_1} > \frac{r_2}{a_2}$;
 - (iv.d) E_2 is a saddle-focus with a 2-dimensional stable manifold and an 1-dimensional unstable manifold if $r_3K > \frac{r_2 + \sqrt{r_2^2 + r_2r_3}}{2a_2}$ and $\frac{r_1}{a_1} < \frac{r_2}{a_2}$;
 - (iv.e) E_2 is a degenerated equilibrium if $\frac{r_2}{a_2} < r_3K$ and $\frac{r_1}{a_1} = \frac{r_2}{a_2}$.
- (v) Each positive equilibrium E_+ is a degenerated equilibrium with a 2-dimensional stable manifold and an 1-dimensional center manifold filled by equilibria.

It is clear that system (1) has three invariant planes $S = 0$, $x_1 = 0$ and $x_2 = 0$, respectively. Our objective is to study the global dynamics of system (1) in \mathbb{R}_+^3 .

However, it is not clear whether or not all solutions of system (1) with positive initial conditions are bounded in forward time. So we must study the equilibria of system (1) at infinity and we shall use the Poincaré compactification of \mathbb{R}_+^3 for doing this study. Note that system (1) defines a polynomial vector field in \mathbb{R}^3 .

Using the Poincaré compactification in \mathbb{R}^3 (see for more details [6]), we consider the unit sphere $\mathbb{S}^3 = \{(y_1, y_2, y_3, y_4) \in \mathbb{R}^4 : \sum_{i=1}^4 y_i^2 = 1\}$ in \mathbb{R}^4 . Its equator is $\mathbb{S}^2 = \{(y_1, y_2, y_3, y_4) \in \mathbb{S}^3 : y_4 = 0\}$. We identify \mathbb{R}^3 with the tangent hyperplane at the north pole of the sphere \mathbb{S}^3 , i.e. at the point $(0, 0, 0, 1)$. Doing central projection of this hyperplane over the sphere \mathbb{S}^3 , \mathbb{R}^3 is identified with the open north hemisphere of \mathbb{S}^3 . Clearly \mathbb{S}^2 is the boundary of this open north hemisphere. The open north hemisphere together with its boundary \mathbb{S}^2 is topologically a closed ball B , whose interior is identified with \mathbb{R}^3 and whose boundary is identified with the infinity of \mathbb{R}^3 . Every point of \mathbb{S}^2 corresponds with one direction for reaching the infinity.

Summarizing system (1) in \mathbb{R}^3 can be extended analytically to a vector field in the closed ball B , called the *Poincaré compactification* of system (1). The infinity \mathbb{S}^2 is invariant under the flow of the extended vector field. The flow on \mathbb{S}^2 is studied taking the local charts defined in [6].

In the local chart U_1 with coordinates

$$S = \frac{1}{z_3}, \quad x_1 = \frac{z_1}{z_3}, \quad x_2 = \frac{z_2}{z_3},$$

system (1) becomes

$$(2) \quad \begin{aligned} \frac{dz_1(t)}{dt} &= a_1 z_1 + \frac{z_1}{K} + b_1 z_1^2 + b_2 z_1 z_2 - r_1 z_1 z_3 - r_3 z_1 z_3, \\ \frac{dz_2(t)}{dt} &= a_2 z_2 + \frac{z_2}{K} + b_1 z_1 z_2 + b_2 z_2^2 - r_2 z_2 z_3 - r_3 z_2 z_3, \\ \frac{dz_3(t)}{dt} &= \frac{z_3}{K} + b_1 z_1 z_3 + b_2 z_2 z_3 - r_3 z_3^2. \end{aligned}$$

The infinity of \mathbb{R}^3 in the local chart U_1 corresponds to the invariant plane $z_3 = 0$ and the infinity of \mathbb{R}_+^3 in the local chart U_1 corresponds to the invariant plane $z_3 = 0$ with $z_1 \geq 0$ and $z_2 \geq 0$. Hence, system (2) in the local chart U_1 has a unique equilibrium at infinity $O_i(0, 0, 0)$. The linear part of system (2) at $O_i(0, 0, 0)$ has eigenvalues $a_1 + \frac{1}{K}$, $a_2 + \frac{1}{K}$ and $\frac{1}{K}$. This implies that equilibrium $O_i(0, 0, 0)$ is an unstable node.

Since the local chart U_1 does not cover the plane $S = 0$ at the infinity of \mathbb{R}^3 , we further consider system (1) in the local chart U_2 with coordinates

$$S = \frac{u_1}{z_3}, \quad x_1 = \frac{1}{z_3}, \quad x_2 = \frac{u_2}{z_3},$$

which becomes

$$(3) \quad \begin{aligned} \frac{du_1(t)}{dt} &= -b_1 u_1 - a_1 u_1^2 - \frac{u_1^2}{K} - b_2 u_1 u_2 + r_1 u_1 z_3 + r_3 u_1 z_3, \\ \frac{du_2(t)}{dt} &= -a_1 u_1 u_2 + a_2 u_1 u_2 + r_1 u_2 z_3 - r_2 u_2 z_3, \\ \frac{dz_3(t)}{dt} &= -a_1 u_1 z_3 + r_1 z_3^2. \end{aligned}$$

Note that all the points on \mathbb{S}^2 at infinity in the coordinates of all local chart have $z_3 = 0$. We are interested only in the equilibria with $u_1 = 0$ and $z_3 = 0$ of system (3), which corresponds to the infinity of \mathbb{R}^3 in the plane $S = 0$ for system (1). If we further restrict at the infinity of \mathbb{R}_+^3 , then system (3) has infinitely many equilibria $E_I(0, u_2, 0)$ with $u_2 \geq 0$ at infinity, which fill up the quarter of a circle on \mathbb{S}^2 . At each equilibrium $E_I(0, u_2, 0)$, system (3) has a double zero eigenvalue and a negative eigenvalue $-(b_1 + b_2 u_2)$ with the eigenvector $\left(\frac{b_1 + b_2 u_2}{(a_1 - a_2)u_2}, 1, 0\right)^T$ in its infinite direction when $a_1 \neq a_2$. The eigenvector associated with the negative eigenvalue when $a_1 = a_2$ is $(1, 0, 0)^T$ in its infinite direction. Obviously, the remaining eigenvalues 0 correspond to eigenvectors going outside the infinity.

Applying the normal hyperbolicity theory (see [8]) first to the local chart U_2 and after to the invariant plane $S = 0$, we obtain that every equilibrium $E_I(0, u_2, 0)$ has an 1-dimensional stable manifold living at infinity (i.e. in \mathbb{S}^2) and two 1-dimensional unstable manifold living in the plane $S = 0$.

On the other hand, it is easy to check that both local charts U_1 and U_2 together have covered all equilibria at the infinity of system (1) in \mathbb{R}_+^3 except the equilibrium point localized at the endpoint of the x_2 -axis in the infinity, but this equilibrium forms part of the line filled of equilibria at infinity. Hence, we can summarize the above analysis as follows.

Proposition 3. *The following two statements hold.*

- (i) *System (1) restricted to the compactification of the octant \mathbb{R}_+^3 has an isolated equilibrium O_i at infinity which is the endpoint of the invariant positive S -axis, and has a line filled of equilibria E_I at infinity which is the end of the invariant plane $S = 0$ intersection with the compactification of the octant \mathbb{R}_+^3 . This line of equilibria fills the quarter of the maximal circle at infinity with endpoints the endpoints of the invariant positive x_1 -axis and x_2 -axis.*
- (ii) *Furthermore O_i is an unstable node and each degenerate equilibria E_I has 1-dimensional stable manifold living at infinity and two 1-dimensional unstable one living in the invariant plane $S = 0$, which is the central manifold of the point E_I . Moreover, the behavior of the flow near these two 1-dimensional manifolds in the finite positive octant is like a hyperbolic sector. The phase portrait of these equilibria on \mathbb{S}^2 is shown in Figure 1.*

Proof. The analysis done before the statement of the proposition has shown the existence and the local phase portraits of these equilibria at infinity. We only need to study the dynamics of system (1) on the center manifold of each equilibria E_I .

Since the positive quadrant of the $x_1 x_2$ -plane is invariant by the flow of system (1) and it is tangent to the center subspaces of each equilibria E_I , the $x_1 x_2$ -plane is the center manifold at each equilibria E_I .

We shall study the phase portrait of system (1) on the positive quadrant of the invariant $x_1 x_2$ -plane. On this plane the flow is determined by

$$(4) \quad \begin{aligned} \frac{dx_1(t)}{dt} &= -r_1 x_1(t), \\ \frac{dx_2(t)}{dt} &= -r_2 x_2(t), \end{aligned}$$

where r_1 and r_2 are positive constants.

It is clear that all solutions of system (4) on the x_1x_2 -plane except the equilibria at infinity will approach to the origin $(0,0,0)$ in forward time. Hence, E_I has two 1-dimensional unstable manifold on its center manifold x_1x_2 -plane. Note that the 1-dimensional stable manifold of E_I is on \mathbb{S}^2 . Hence, the phase portrait in the finite part and near each equilibria E_I looks like a saddle. And the isolated equilibrium O_i is an unstable node. Thus, we can sketch the phase portraits near all equilibria at infinity of system (4) on \mathbb{S}^2 and on $S = 0$ in Figure 1. \square

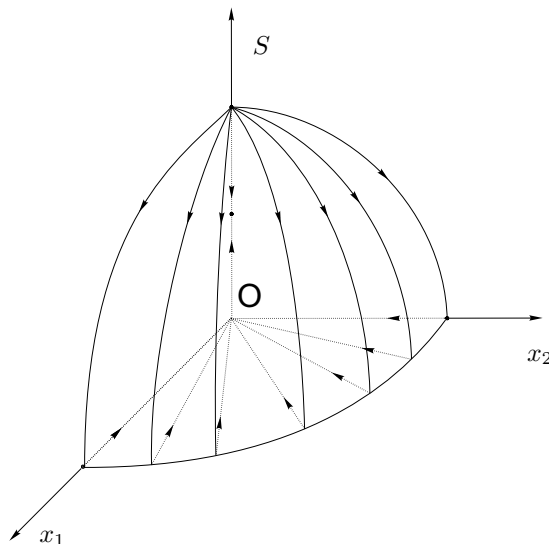


FIGURE 1. The phase portrait of system (1) near all equilibria at infinity on \mathbb{S}^2 .

In the following, we analytically establish that all solutions of system (1) with positive initial conditions are bounded in forward time. This shows that system (1) is “well behaved” as one intuit from the biological problem.

Theorem 4. *All orbits of system (1) with positive initial conditions are positive and bounded.*

Proof. Since the flow of system (1) is invariant in the three coordinate planes of \mathbb{R}_+^3 , all trajectories of system (1) with positive initial conditions remains in \mathbb{R}_+^3 . From Proposition 3, we know that all equilibria at infinity of system (1) in its finite direction are repeller. Therefore, all trajectories of system (1) with positive initial conditions cannot reach the infinity. This implies that every trajectory is bounded. \square

2.2. Global dynamics. First we show that system (1) allows the coexistence of two competing predators for some values of parameters, which implies that the coexistence of two predators competing for a single prey species is possible when the predator functional response to the prey density is linear. And for some other values of parameters, both two competing predators go extinction and only prey survives.

Theorem 5. *If $\frac{r_1}{a_1} = \frac{r_2}{a_2}$, then system (1) has a first integral $F(S, x_1, x_2) = c$, where $F(S, x_1, x_2) = x_1^{a_2} x_2^{-a_1}$ and c is any a constant. Furthermore*

- (i) *if $r_3 K > \frac{r_1}{a_1}$, then on the invariant surface $F(S, x_1, x_2) = c$ with $c > 0$ in $\text{Int}(\mathbb{R}_+^3)$, system (1) has a unique positive equilibrium $E_+(\frac{r_1}{a_1}, (cx_2^{a_1})^{\frac{1}{a_2}}, x_2)$, which is a global attractor on $\{F(S, x_1, x_2) = c\} \cap \text{Int}(\mathbb{R}_+^3)$;*
- (ii) *if $r_3 K \leq \frac{r_1}{a_1}$, then on the invariant surface $F(S, x_1, x_2) = c$ with $c > 0$ in $\text{Int}(\mathbb{R}_+^3)$, system (1) has not any equilibria and all orbits of (1) approach to a boundary point $(r_3 K, 0, 0)$ of this invariant surface in forward time.*

Proof. Since the function $F(S, x_1, x_2)$ satisfies

$$\left. \frac{dF(S, x_1, x_2)}{dt} \right|_{(1)} = a_1 a_2 \left(\frac{r_2}{a_2} - \frac{r_1}{a_1} \right) F(S, x_1, x_2),$$

$\left. \frac{dF(S, x_1, x_2)}{dt} \right|_{(1)} = 0$ as $\frac{r_1}{a_1} = \frac{r_2}{a_2}$. Hence, $F(S, x_1, x_2)$ is a first integral of system (1) by definition of the first integral.

Let

$$F(S, x_1, x_2) = c, \quad c > 0.$$

Then the invariant surface, $F(S, x_1, x_2) = c$, of system (1) foliates $\text{Int}\mathbb{R}_+^3$. Obviously, the intersection of the invariant surface $F(S, x_1, x_2) = c$ and the invariant $x_1 x_2$ -plane is an orbit of system (1). And the intersection of the invariant surface and a given plane $S = \alpha$ with $\alpha > 0$ in $\text{Int}\mathbb{R}_+^3$ is a curve. It is easy to check that this curve is monotone function of x_1 or x_2 .

We first prove statement (i). If $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ and $r_3 K > \frac{r_1}{a_1}$, then from proposition 1, we know that system (1) has infinitely many positive equilibria $E_+(S, x_1, x_2)$ which fill up a segment L ,

$$L = \left\{ (S, x_1, x_2) : S = \frac{r_1}{a_1}, \quad b_1 x_1 + b_2 x_2 = r_3 K - \frac{r_1}{a_1}, \quad x_1 \geq 0, \quad x_2 \geq 0 \right\}.$$

Therefore, the surface $F(S, x_1, x_2) = c$ must cross L at exact one point on the plane $S = \frac{r_1}{a_1}$.

Note that the flow of system (1) is invariant on each foliation $F(S, x_1, x_2) = c$ with $c > 0$. Thus, the global dynamics of system (1) in $\text{Int}\mathbb{R}_+^3$ is equivalent to that of system (1) restricted on each foliation $F(S, x_1, x_2) = c$ of $\text{int}\mathbb{R}_+^3$.

In what follows, we consider the restricted system

$$(5) \quad \begin{aligned} \frac{dS(t)}{dt} &= S(t) \left(r_3 - \frac{1}{K} S(t) - b_1 (cx_2^{a_1}(t))^{\frac{1}{a_2}} - b_2 x_2(t) \right), \\ \frac{dx_2(t)}{dt} &= x_2(t) (-r_2 + a_2 S(t)). \end{aligned}$$

From the above analysis, we know that system (5) has a unique positive equilibrium at $(\frac{r_1}{a_1}, x_2^+)$, where x_2^+ is a unique positive solution of

$$b_1 (cx_2^{a_1})^{\frac{1}{a_2}} + b_2 x_2 = r_3 - \frac{r_1}{a_1 K}.$$

By computing the Jacobian matrix of system (5) at $(\frac{r_1}{a_1}, x_2^+)$, we have that its two eigenvalues have negative real parts. Hence, the equilibrium is local asymptotically stable on the foliation.

By Theorem 4, we know that every solution of system (5) is positive and bounded in the foliation. We next prove that the positive equilibrium at $(\frac{r_1}{a_1}, x_2^+)$ is global stable in the foliation. Otherwise we assume that system (5) has a non-trivial periodic solution $\gamma(t)$ with period T which is the first closed orbit near the positive equilibrium $(\frac{r_1}{a_1}, x_2^+)$,

$$\gamma(t) = \{(S, x_2) : S = S(t) > 0, x_2 = x_2(t) > 0, 0 \leq t \leq T\}.$$

Then by (5) we have

$$(6) \quad \begin{aligned} 0 &= \ln \frac{S(T)}{S(0)} = \int_0^T \frac{dS(t)}{S(t)} = \int_0^T \left(r_3 - \frac{1}{K}S(t) - b_1(cx_2^{a_1}(t))^{\frac{1}{a_2}} - b_2x_2(t) \right) dt, \\ 0 &= \ln \frac{x_2(T)}{x_2(0)} = \int_0^T \frac{dx_2(t)}{x_2(t)} = \int_0^T (-r_2 + a_2S(t)) dt, \end{aligned}$$

where $(S(t), x_2(t))$ is the non-trivial periodic solution $\gamma(t)$ of system (5).

In the following we consider the stability of $\gamma(t)$. We calculate the integral of divergence of vector field (5) along the periodic solution $\gamma(t)$.

$$\begin{aligned} \oint_{\gamma(t)} \text{div}(5) dt &= \int_0^T \left(r_3 - \frac{2}{K}S(t) - b_1(cx_2^{a_1}(t))^{\frac{1}{a_2}} - b_2x_2(t) + (-r_2 + a_2S(t)) \right) dt \\ &= \int_0^T -\frac{1}{K}S(t) dt < 0 \end{aligned}$$

by (6). Therefore, the periodic solution $\gamma(t)$ is stable. On the other hand, the unique equilibrium is local asymptotically stable on the foliation. This leads to a contradiction. Thus, the non-trivial periodic solution $\gamma(t)$ does not exist, which implies that the positive equilibrium at $(\frac{r_1}{a_1}, x_2^+)$ is global stable in the foliation. Hence statement (i) holds.

In the following we consider the case that $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ and $r_3K \leq \frac{r_1}{a_1}$. From Proposition 1, we know that system (1) has not any equilibria in $\text{Int}\mathbb{R}_+^3$. Hence, there do not exist periodic solutions of system (1) on the invariant surface $F(S, x_1, x_2) = c$.

It is clear that the global dynamics of system (1) in $\text{Int}\mathbb{R}_+^3$ is equivalent to that of system (5) on the invariant surface. And all solutions of system (5) in $\text{Int}\mathbb{R}_+^3$ are bounded. On the boundary of the invariant surface $F(S, x_1, x_2) = c$, system (5) has two equilibria at $(0, 0)$ and $(r_3K, 0)$, respectively. The equilibrium $(r_3K, 0)$ is a stable node and $(0, 0)$ is a saddle with 1-dimensional stable manifold $\{F(S, x_1, x_2) = c\} \cap \{(S, x_1, x_2) : S = 0\}$ and 1-dimensional unstable manifold $\{(S, x_1, x_2) : x_1 = 0, x_2 = 0, 0 < S < r_3K\}$. Hence, all solutions of system (5) with positive initial conditions approach to equilibrium $(r_3K, 0)$ in forward time. This proves statement (ii). \square

Theorem 5 has shown the dynamics of system (1) in $\text{Int}\mathbb{R}_+^3$ if $\frac{r_1}{a_1} = \frac{r_2}{a_2}$. To obtain the global dynamics of system (1) in \mathbb{R}_+^3 , we need to consider the dynamics of system (1) on the three invariant coordinate planes. Note that system (1) restricted on the invariant x_1x_2 -plane has a unique equilibrium $(0, 0)$ which is global stable for all parameters. We only consider the dynamics of system (1) on the invariant Sx_1 -plane and on the invariant Sx_2 -plane, respectively.

On the invariant Sx_1 -plane, the restricted system of (1) is

$$(7) \quad \begin{aligned} \frac{dS(t)}{dt} &= S(t) \left(r_3 - \frac{1}{K}S(t) - b_1x_1(t) \right), \\ \frac{dx_1(t)}{dt} &= x_1(t) (-r_1 + a_1S(t)). \end{aligned}$$

And on the invariant Sx_2 -plane, the restricted system of (1) is

$$(8) \quad \begin{aligned} \frac{dS(t)}{dt} &= S(t) \left(r_3 - \frac{1}{K}S(t) - b_2x_2(t) \right), \\ \frac{dx_2(t)}{dt} &= x_2(t) (-r_2 + a_2S(t)). \end{aligned}$$

From the knowledge of the 2-dimensional Lotka–Volterra system, it follows easily the next result.

Proposition 6. *The following two statements hold.*

- (i) *If $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ and $r_3K > \frac{r_1}{a_1}$, then system (7) and system (8) has three equilibria at $(0, 0)$, $(r_3K, 0)$ and $(\frac{r_1}{a_1}, \frac{1}{b_1}(r_3 - \frac{r_1}{Ka_1}))$, where $(0, 0)$ and $(r_3K, 0)$ are saddles, and $(\frac{r_1}{a_1}, \frac{1}{b_1}(r_3 - \frac{r_1}{Ka_1}))$ is a stable node or focus, which attracts all orbits of (7) and (8) in the interior of the Sx_1 -plane and of the Sx_2 -plane, respectively;*
- (ii) *If $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ and $r_3K \leq \frac{r_1}{a_1}$, then system (7) and system (8) has two equilibria at $(0, 0)$ and $(r_3K, 0)$, where $(0, 0)$ is saddle, and $(r_3K, 0)$ is a stable node, which attracts all orbits of (7) and (8) in the interior of the Sx_1 -plane and of the Sx_2 -plane, respectively;*

Summarizing Theorem 5 and Proposition 6 we obtain:

Theorem 7. *The following two statements hold.*

- (i) *If $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ and $r_3K > \frac{r_1}{a_1}$, then system (1) has infinitely many positive equilibria $E_+(S, x_1, x_2)$ filling up a segment L which attract all solutions of system (1) with positive initial conditions, the endpoints of L attract all solutions of system (1) with nonnegative initial conditions $(S, x_1, 0)$ or $(S, 0, x_2)$, respectively, and the origin $(0, 0, 0)$ attracts all solutions of system (1) with nonnegative initial conditions $(0, x_1, x_2)$. The phase portrait is shown in Figure 2.*
- (ii) *If $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ and $r_3K \leq \frac{r_1}{a_1}$, then system (1) has only two equilibria $(0, 0, 0)$ and $(r_3K - \frac{r_1}{a_1}, 0, 0)$, the equilibrium $(r_3K - \frac{r_1}{a_1}, 0, 0)$ attracts all solutions of system (1) except the orbits in the x_1x_2 -plane, and the equilibrium $(0, 0, 0)$ attracts all solutions of system (1) in the x_1x_2 -plane. The phase portrait is sketched in Figure 3.*

Theorem 7 makes sense biologically, which reveals that two competing predators either coexist or co-extinct if they have the same ratio of death rate and propagation rate. When the ratio of death rate and propagation rate of the predator is less than the product of the birth rate and the carrying capacity of the prey, two competing predators coexist at a positive equilibrium. However, if the ratio of death rate and of the propagation rate of the predator is more large than the product of the birth rate and the carrying capacity of the prey, then the two competing predators

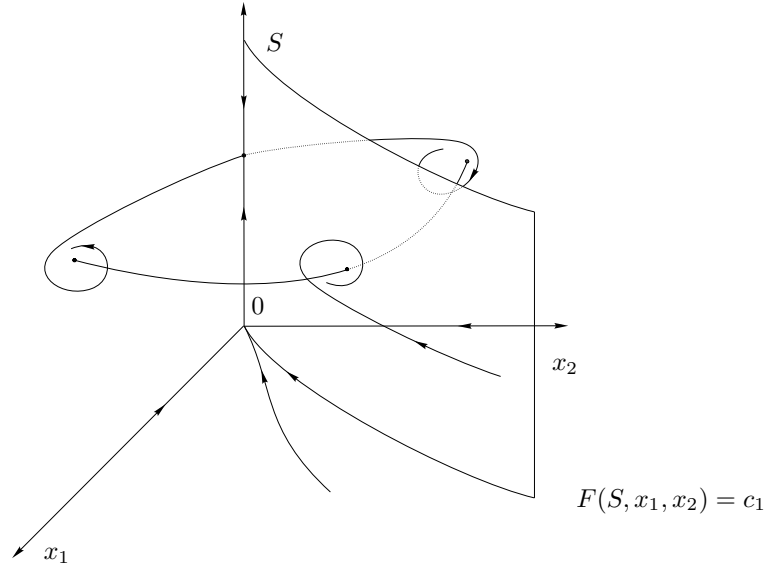


FIGURE 2. *Global dynamics of system (1) when $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ and $r_3K > \frac{r_1}{a_1}$.*

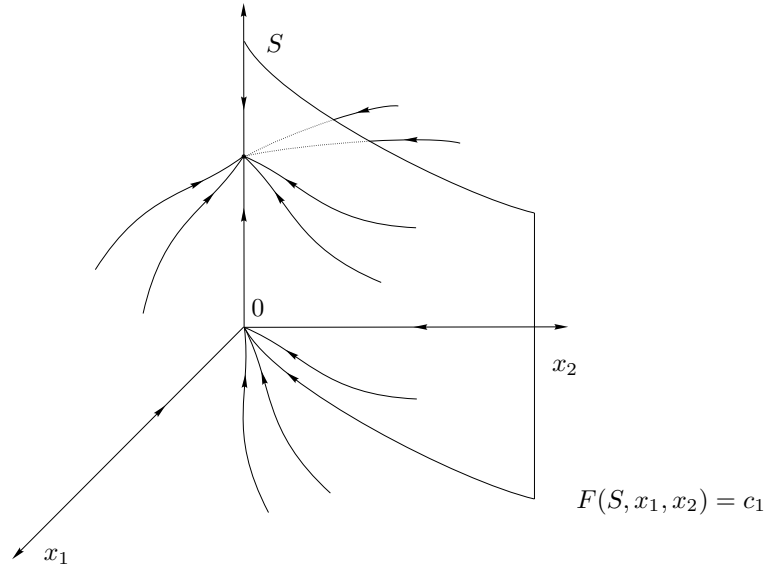


FIGURE 3. *Global dynamics of system (1) when $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ and $r_3K \leq \frac{r_1}{a_1}$.*

species eventually become extinct even though prey persists. This coincides with our intuition but conflicts with the principle of competitive exclusion.

In what follows we consider if there exists some values of parameters such that the principle of competitive exclusion holds for system (1). We first give the dynamics of system (1) in $\text{Int}\mathbb{R}_+^3$.

Theorem 8. *If $\frac{r_1}{a_1} \neq \frac{r_2}{a_2}$, then the principle of competitive exclusion may hold for system (1). More precisely,*

- (i) *if $\frac{r_1}{a_1} > \frac{r_2}{a_2}$, then all orbits of system (1) in $\text{Int}(\mathbb{R}_+^3)$ are asymptotic to the orbits on the Sx_2 -plane in forward time;*
- (ii) *if $\frac{r_1}{a_1} < \frac{r_2}{a_2}$, then all orbits of system (1) in $\text{Int}(\mathbb{R}_+^3)$ are asymptotic to the orbits on the Sx_1 -plane in forward time.*

Proof. Let the set \mathcal{D} be the intersection of the Poincaré compactification ball B and \mathbb{R}_+^3 , that is $\mathcal{D} = B \cap \mathbb{R}_+^3$.

We choose a sufficient large compact set $D_1, D_1 \subset \mathcal{D}$, such that D_1 does not include $x_2 = 0$, and we choose a sufficient large compact set $D_2, D_2 \subset \mathcal{D}$, such that D_2 does not include $x_1 = 0$.

From Theorem 4 we know that D_1 and D_2 are positive invariant sets of system (1), that is, any solutions $(S(t), x_1(t), x_2(t))$ of system (1) with the initial point $(S(t_0), x_1(t_0), x_2(t_0))$ in D_1 or in D_2 will stay in D_1 or in D_2 , respectively, for all $t \geq t_0$.

To prove statement (i) we consider the function

$$V_1(S, x_1, x_2) = x_1^{a_2} x_2^{-a_1}.$$

Clearly, $V_1(S, x_1, x_2)$ is a continuous differential function in D_1 . And

$$\left. \frac{dV_1(S, x_1, x_2)}{dt} \right|_{(1)} = a_1 a_2 \left(\frac{r_2}{a_2} - \frac{r_1}{a_1} \right) V_1(S, x_1, x_2) \leq 0,$$

because $\frac{r_1}{a_1} > \frac{r_2}{a_2}$. Hence, the solutions $(S(t), x_1(t), x_2(t))$ of system (1) with the initial point $(S(t_0), x_1(t_0), x_2(t_0))$ in D_1 satisfies

$$x_1^{a_2}(t) x_2^{-a_1}(t) = x_1^{a_2}(t_0) x_2^{-a_1}(t_0) e^{a_1 a_2 t \left(\frac{r_2}{a_2} - \frac{r_1}{a_1} \right)}.$$

Let

$$D_{10} = \left\{ (S, x_1, x_2) : \left. \frac{dV_1(S, x_1, x_2)}{dt} \right|_{(1)} = 0, (S, x_1, x_2) \in D_1 \right\}.$$

Then

$$D_{10} = \{(S, x_1, x_2) : x_1 = 0\},$$

which is an invariant set of system (1). By LaSalle Principle, we know that all solutions of system (1) in D_1 are asymptotic to the orbits on the Sx_2 -plane in forward time, which leads to statement (i).

Using similar arguments we can obtain statement (ii) by choosing the function

$$V_2(S, x_1, x_2) = x_1^{-a_2} x_2^{a_1}$$

in D_2 . This ends the proof. \square

When $\frac{r_1}{a_1} \neq \frac{r_2}{a_2}$, almost all orbits of system (1) are asymptotic to some orbits on the Sx_1 -plane or on the Sx_2 -plane in forward time. But we do not know what kinds of orbits on the Sx_1 -plane or on the Sx_2 -plane are the asymptotic ones. To characterize the principle of competitive exclusion holding for system (1), we have

to show that one of two competing predators must be extinct and the other predator must survive. So we consider the dynamics of system (1) on the invariant Sx_1 -plane and on the invariant Sx_2 -plane, respectively.

From Proposition 2 and the knowledge of the 2-dimensional Lotka-Volterra system, we have

Proposition 9. *If $\frac{r_1}{a_1} \neq \frac{r_2}{a_2}$, then the following statements hold.*

- (i) *If either $r_3K > \frac{r_1}{a_1} > \frac{r_2}{a_2}$, or $r_3K > \frac{r_2}{a_2} > \frac{r_1}{a_1}$, then system (7) (or (8)) has three equilibria at $(0,0)$, $(r_3K,0)$ and $(\frac{r_1}{a_1}, \frac{1}{b_1}(r_3 - \frac{r_1}{Ka_1}))$ (or $(\frac{r_2}{a_2}, \frac{1}{b_2}(r_3 - \frac{r_2}{Ka_2}))$), respectively, where $(0,0)$ and $(r_3K,0)$ are saddles, and $(\frac{r_1}{a_1}, \frac{1}{b_1}(r_3 - \frac{r_1}{Ka_1}))$ ($(\frac{r_2}{a_2}, \frac{1}{b_2}(r_3 - \frac{r_2}{Ka_2}))$), respectively is a stable node or focus, which attracts all orbits of (7) ((8), respectively) in the interior of the Sx_1 -plane (Sx_2 -plane, respectively).*
- (ii) *If $\frac{r_2}{a_2} < r_3K \leq \frac{r_1}{a_1}$, then system (7) has two equilibria at $(0,0)$ and $(r_3K,0)$, where $(0,0)$ is a saddle and $(r_3K,0)$ is a stable node, which attracts all orbits of (7) in the interior of the Sx_1 -plane. And system (8) has three equilibria at $(0,0)$, $(r_3K,0)$ and $(\frac{r_2}{a_2}, \frac{1}{b_2}(r_3 - \frac{r_2}{Ka_2}))$, where $(0,0)$ and $(r_3K,0)$ are saddles, and $(\frac{r_2}{a_2}, \frac{1}{b_2}(r_3 - \frac{r_2}{Ka_2}))$ is a stable node or focus, which attracts all orbits of (8) in the interior of the Sx_2 -plane, respectively.*
- (iii) *If $\frac{r_1}{a_1} < r_3K \leq \frac{r_2}{a_2}$, then system (8) has two equilibria at $(0,0)$ and $(r_3K,0)$, where $(0,0)$ is a saddle and $(r_3K,0)$ is a stable node, which attracts all orbits of (8) in the interior of the Sx_2 -plane. And system (7) has three equilibria at $(0,0)$, $(r_3K,0)$ and $(\frac{r_1}{a_1}, \frac{1}{b_1}(r_3 - \frac{r_1}{Ka_1}))$, where $(0,0)$ and $(r_3K,0)$ are saddles, and $(\frac{r_1}{a_1}, \frac{1}{b_1}(r_3 - \frac{r_1}{Ka_1}))$ is a stable node or focus, which attracts all orbits of (7) in the interior of the Sx_1 -plane, respectively.*
- (iv) *If either $r_3K \leq \frac{r_2}{a_2} < \frac{r_1}{a_1}$ or $r_3K \leq \frac{r_1}{a_1} < \frac{r_2}{a_2}$, then system (7) and system (8) has two equilibria at $(0,0)$ and $(r_3K,0)$, where $(0,0)$ is a saddle, and $(r_3K,0)$ is a stable node, which attracts all orbits of (7) and (8) in the interior of the Sx_1 -plane and of the Sx_2 -plane, respectively;*

To summarize Theorem 8 and Proposition 9, we give the sufficient and necessary conditions to guarantee that the principle of competitive exclusion holds for system (1) as follows.

Theorem 10. *The principle of competitive exclusion holds for system (1) if and only if one of the following conditions holds.*

- (i) $r_3K > \frac{r_1}{a_1} > \frac{r_2}{a_2}$. *In this case the predator species $x_1(t)$ goes to extinction and the predator species $x_2(t)$ survives.*
- (ii) $\frac{r_2}{a_2} < r_3K \leq \frac{r_1}{a_1}$. *In this case the predator species $x_1(t)$ goes to extinction and the predator species $x_2(t)$ survives.*
- (iii) $r_3K > \frac{r_2}{a_2} > \frac{r_1}{a_1}$. *In this case the predator species $x_2(t)$ goes to extinction and the predator species $x_1(t)$ survives.*
- (iv) $\frac{r_1}{a_1} < r_3K \leq \frac{r_2}{a_2}$. *In this case the predator species $x_2(t)$ goes to extinction and the predator species $x_1(t)$ survives.*

The principle of competitive exclusion does not hold for system (1) if either $r_3K \leq \frac{r_2}{a_2} < \frac{r_1}{a_1}$, or $r_3K \leq \frac{r_1}{a_1} < \frac{r_2}{a_2}$. In this case both two competing predators go to

extinction, and all orbits of system (1) are asymptotic to the equilibrium $(r_3 K, 0, 0)$ except the orbits on the $x_1 x_2$ -plane.

3. GLOBAL DYNAMICS OF SYSTEM (1) WITH UNLIMITED RESOURCE FOR PREY

In the section we study system (1) with $K = +\infty$ in \mathbb{R}_+^3 , i.e. the system

$$(9) \quad \begin{aligned} \frac{dS(t)}{dt} &= S(t) (r_3 - b_1 x_1(t) - b_2 x_2(t)), \\ \frac{dx_1(t)}{dt} &= x_1(t) (-r_1 + a_1 S(t)), \\ \frac{dx_2(t)}{dt} &= x_2(t) (-r_2 + a_2 S(t)). \end{aligned}$$

In a similar way to section 2 we first give the existence and topological classification of the finite equilibria and the equilibria at infinity for system (9), then we study the global dynamics of this system.

3.1. The existence and topological classification of equilibria. It is clear that system (9) has three equilibria the origin $O(0, 0, 0)$, $\hat{E}_1 \left(\frac{r_1}{a_1}, \frac{r_3}{b_1}, 0 \right)$ and $\hat{E}_2 \left(\frac{r_2}{a_2}, 0, \frac{r_3}{b_2} \right)$ in \mathbb{R}_+^3 for all the values of the parameters. Except these equilibria, system (9) may have a positive equilibrium in \mathbb{R}_+^3 for some values of parameters. Doing easy algebra calculations we obtain the following result.

Proposition 11. *System (9) has a positive equilibrium $\hat{E}_+(S, x_1, x_2)$ in $\text{Int}(\mathbb{R}_+^3)$ if and only if $\frac{r_1}{a_1} = \frac{r_2}{a_2}$. And if system (9) has a positive equilibrium in $\text{Int}(\mathbb{R}_+^3)$, then system (9) has infinitely many positive equilibria $\hat{E}_+(S, x_1, x_2)$ in $\text{Int}(\mathbb{R}_+^3)$, which fill up a segment L_0 with endpoints \hat{E}_1 and \hat{E}_2 , where*

$$L_0 = \left\{ (S, x_1, x_2) : S = \frac{r_1}{a_1}, b_1 x_1 + b_2 x_2 = r_3, x_1 \geq 0, x_2 \geq 0 \right\}.$$

We now study the local phase portraits of the boundary equilibria and positive equilibria. Since the Jacobian matrix $J_1(S, x_1, x_2)$ of system (9) at an equilibrium (S, x_1, x_2) is

$$J_1(S, x_1, x_2) = \begin{pmatrix} r_3 - b_1 x_1 - b_2 x_2 & -b_1 S & -b_2 S \\ a_1 x_1 & -r_1 + a_1 S & 0 \\ a_2 x_2 & 0 & -r_2 + a_2 S \end{pmatrix},$$

we obtain the following local phase portraits for the equilibria after some computations and the applications of the standard results.

Proposition 12. *The following statements hold.*

- (i) $O(0, 0, 0)$ is a saddle with a 2-dimensional stable manifold and an 1-dimensional unstable manifold for all parameters.
- (ii) $\hat{E}_1 \left(\frac{r_1}{a_1}, \frac{r_3}{b_1}, 0 \right)$ has the following local phase portraits depending on the values of the parameters.
 - (ii.a) \hat{E}_1 is a non-hyperbolic equilibrium with an 1-dimensional stable manifold and a 2-dimensional center manifold if $\frac{r_1}{a_1} < \frac{r_2}{a_2}$;
 - (ii.b) \hat{E}_1 is a zero-Hopf equilibrium with a 3-dimensional center manifold if $\frac{r_1}{a_1} = \frac{r_2}{a_2}$;

- (ii.c) \hat{E}_1 is a non-hyperbolic equilibrium with an 1-dimensional unstable manifold and a 2-dimensional center manifold if $\frac{r_1}{a_1} > \frac{r_2}{a_2}$.
- (iii) $\hat{E}_2 \left(\frac{r_2}{a_2}, 0, \frac{r_3}{b_2} \right)$ has the following local phase portraits depending on the values of the parameters.
 - (iii.a) \hat{E}_2 is a non-hyperbolic equilibrium with an 1-dimensional unstable manifold and a 2-dimensional center manifold if $\frac{r_1}{a_1} < \frac{r_2}{a_2}$;
 - (iii.b) \hat{E}_2 is a zero-Hopf equilibrium with a 3-dimensional center manifold if $\frac{r_1}{a_1} = \frac{r_2}{a_2}$;
 - (iii.c) \hat{E}_2 is a non-hyperbolic equilibrium with an 1-dimensional stable manifold and a 2-dimensional center manifold if $\frac{r_1}{a_1} > \frac{r_2}{a_2}$.
- (iv) Each positive equilibrium \hat{E}_+ is a zero-Hopf equilibrium with 3-dimensional center manifold.

It is clear that system (9) has three invariant planes $S = 0$, $x_1 = 0$ and $x_2 = 0$, respectively. Our objective is to study the global dynamics of system (9) in \mathbb{R}_+^3 . However, it is not clear whether or not all solutions of system (9) with positive initial conditions are bounded in forward time. So we must study the equilibria of system (9) at infinity. Using the Poincaré compactification of \mathbb{R}_+^3 and similar arguments to those of section 2, we obtain the following result

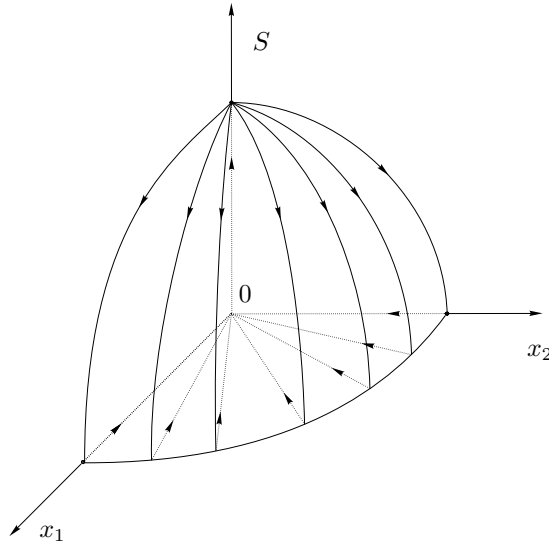


FIGURE 4. The phase portrait of system (9) near all equilibria at infinity on \mathbb{S}^2 .

Proposition 13. *The following two statements hold.*

- (i) System (9) restricted to the compactification of the octant \mathbb{R}_+^3 has an isolated equilibrium \hat{O}_i at infinity which is the endpoint of the invariant positive S -axis, and has a line filled of equilibria \hat{E}_I at infinity which is the end of

the invariant plane $S = 0$ intersection with the compactification of the octant \mathbb{R}_+^3 . This line of equilibria fills the quarter of the maximal circle at infinity with the endpoints of the invariant positive x_1 -axis and x_2 -axis.

- (ii) Furthermore, \hat{O}_i is degenerate with two dimensional unstable manifolds and one dimensional center manifold living in the invariant S -axis, and each degenerate equilibria \hat{E}_I has 1-dimensional stable manifold living at infinity and two 1-dimensional unstable ones living in the invariant plane $S = 0$, which is the central manifold of the point \hat{E}_I . Moreover, the behavior of the flow near these two 1-dimensional manifolds in the finite positive octant is like a hyperbolic sector. The phase portrait of these equilibria on \mathbb{S}^2 is shown in Figure 4.

According to Proposition 13 we get the next result.

Theorem 14. *All orbits of system (9) with positive initial conditions are positive and bounded.*

3.2. Global dynamics of system (9). From Proposition 11, we know that system (9) has positive equilibria if and only if $\frac{r_1}{a_1} = \frac{r_2}{a_2}$. Thus, we discuss the global dynamics of system (9) depending on the relation between of $\frac{r_1}{a_1}$ and $\frac{r_2}{a_2}$.

Theorem 15. *The following statements hold for the solutions of system (9) with positive initial values.*

- (i) *If $\frac{r_1}{a_1} > \frac{r_2}{a_2}$, then all orbits of system (9) in $\text{Int}(\mathbb{R}_+^3)$ are asymptotic to some orbits on the Sx_2 -plane in forward time, and all orbits on the Sx_2 -plane are closed orbits except the equilibrium $\hat{E}_2\left(\frac{r_2}{a_2}, 0, \frac{r_3}{b_2}\right)$. The phase portrait of system (9) in $\text{Int}(\mathbb{R}_+^3)$ is shown in Figure 5.*
- (ii) *If $\frac{r_1}{a_1} = \frac{r_2}{a_2}$, then system (9) in $\text{Int}\mathbb{R}_+^3$ has two independent first integrals $F(S, x_1, x_2) = c_1$ and $G(S, x_1, x_2) = c_2$, which completely determines the dynamics of system (9) in $\text{Int}\mathbb{R}_+^3$, where $F(S, x_1, x_2) = x_1^{a_2} x_2^{-a_1}$,*

$$G(S, x_1, x_2) = \frac{b_1}{a_1} x_1 + \frac{b_2}{a_2} x_2 + S - \frac{r_3}{a_1} \ln x_1 - \frac{r_1}{a_1} \ln S,$$

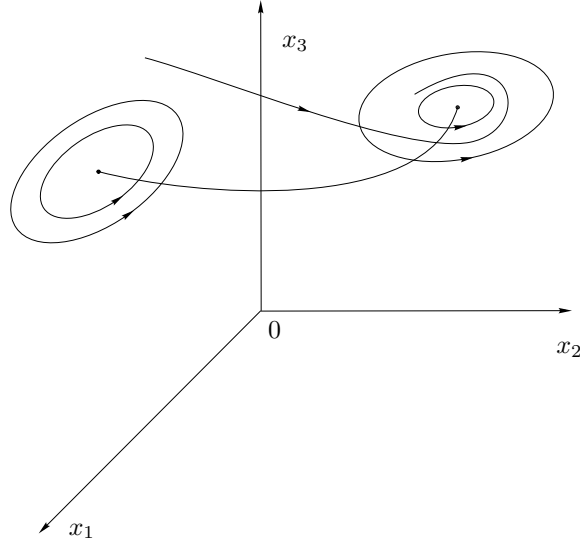
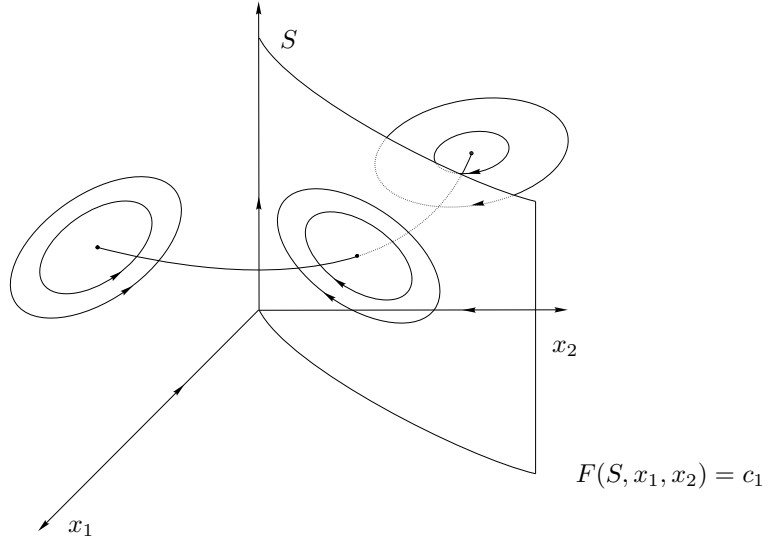
and c_1 and c_2 are arbitrary constants. Furthermore, all orbits of system (9) are closed orbits except \hat{E}_+ . The phase portrait of system (9) in $\text{Int}(\mathbb{R}_+^3)$ is shown in Figure 6.

- (iii) *If $\frac{r_1}{a_1} < \frac{r_2}{a_2}$, then all orbits of system (9) in $\text{Int}(\mathbb{R}_+^3)$ are asymptotic to the orbits on the Sx_1 -plane in forward time, and all orbits on the Sx_1 -plane are closed orbits except the equilibrium $\hat{E}_1\left(\frac{r_1}{a_1}, \frac{r_3}{b_1}, 0\right)$. The phase portrait of system (9) in $\text{Int}(\mathbb{R}_+^3)$ is shown in Figure 7.*

Proof. Using arguments similar to the ones of the proof of Theorem 8, the fact that $\hat{E}_2\left(\frac{r_2}{a_2}, 0, \frac{r_3}{b_2}\right)$ is a center on the Sx_2 -plane, and $\hat{E}_1\left(\frac{r_1}{a_1}, \frac{r_3}{b_1}, 0\right)$ is a center on the Sx_1 -plane, we can obtain statements (i) and (iii). Hence, we only need to prove statement (ii).

Since the function $F(S, x_1, x_2)$ satisfies

$$\left. \frac{dF(S, x_1, x_2)}{dt} \right|_{(9)} = a_1 a_2 \left(\frac{r_1}{a_1} - \frac{r_2}{a_2} \right) F(S, x_1, x_2),$$

FIGURE 5. *Global dynamics of system (9) when $\frac{r_1}{a_1} > \frac{r_2}{a_2}$.*FIGURE 6. *Global dynamics of system (9) when $\frac{r_1}{a_1} = \frac{r_2}{a_2}$.*

$\left. \frac{dF(S, x_1, x_2)}{dt} \right|_{(9)} \equiv 0$ in $\text{Int}(\mathbb{R}_+^3)$ if and only if $\frac{r_1}{a_1} = \frac{r_2}{a_2}$. Hence, $F(S, x_1, x_2) = c_1$ is a first integral of system (9) by definition of the first integral, where c_1 is any a constant.

And the function $G(S, x_1, x_2)$ satisfies

$$\left. \frac{dG(S, x_1, x_2)}{dt} \right|_{(9)} = b_2 \left(\frac{r_1}{a_1} - \frac{r_2}{a_2} \right) x_2,$$

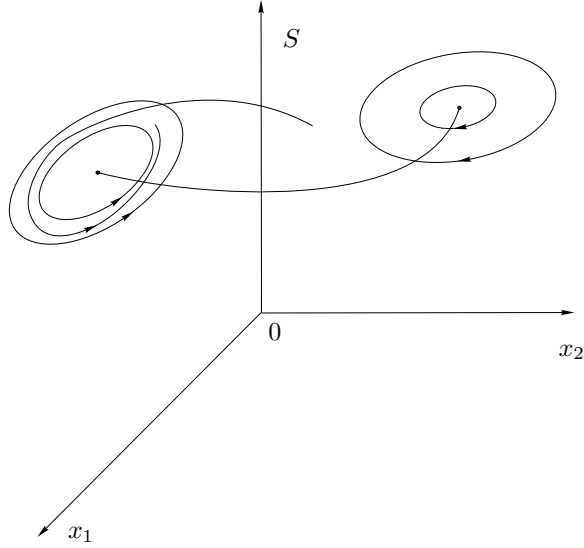


FIGURE 7. Global dynamics of system (9) when $\frac{r_1}{a_1} < \frac{r_2}{a_2}$.

$\left. \frac{dG(S, x_1, x_2)}{dt} \right|_{(9)} \equiv 0$ in $\text{Int}(\mathbb{R}_+^3)$ if and only if $\frac{r_1}{a_1} = \frac{r_2}{a_2}$. Hence, $G(S, x_1, x_2) = c_2$ is the other first integral of system (9) by definition of the first integral, where c_2 is any a constant.

It can be checked that the two functions, $F(S, x_1, x_2)$ and $G(S, x_1, x_2)$, are functionally independent. Thus, system (9) has two independent first integrals, which implies that system (9) is completely integrable, and all orbits of system (9) in $\text{Int}\mathbb{R}_+^3$ are the intersection curves of the invariant surface $F(S, x_1, x_2) = c_1$ and the invariant surface $G(S, x_1, x_2) = c_2$ in $\text{Int}\mathbb{R}_+^3$.

Let

$$F(S, x_1, x_2) = c_1, \quad c_1 > 0.$$

Then the invariant surfaces, $F(S, x_1, x_2) = c_1$, of system (9) foliate the interior of the first octant (i.e. $\text{Int}\mathbb{R}_+^3$). On each leaf $F(S, x_1, x_2) = c_1$, system (9) has a unique positive equilibrium $\hat{E}_+(\frac{r_1}{a_1}, x_1, x_2)$ satisfying $x_1 = (c_1 x_2^{a_1})^{\frac{1}{a_2}}$ and $b_1 x_1 + b_2 x_2 = r_3$. We will demonstrate analytically that each leaf is filled with periodic orbits of system (9) and unique the positive equilibrium \hat{E}_+ in $\text{Int}\mathbb{R}_+^3$.

Note that the flow of system (9) is invariant on each foliation $F(S, x_1, x_2) = c_1$ with $c_1 > 0$. Thus, the global dynamics of system (9) in $\text{Int}\mathbb{R}_+^3$ is equivalent to that of system (9) restricted on each foliation $F(S, x_1, x_2) = c_1$ for any a $c_1 > 0$.

We now consider the restricted system

$$(10) \quad \begin{aligned} \frac{dS(t)}{dt} &= S(t) \left(r_3 - b_1 (c_1 x_2^{a_1}(t))^{\frac{1}{a_2}} - b_2 x_2(t) \right), \\ \frac{dx_2(t)}{dt} &= x_2(t) (-r_2 + a_2 S(t)). \end{aligned}$$

From the above analysis, we know that system (10) has a unique positive equilibrium at $(\frac{r_2}{a_2}, x_2^+)$, where x_2^+ is the unique positive solution of

$$b_1(c_1 x_2^{a_1})^{\frac{1}{a_2}} + b_2 x_2 = r_3.$$

By computing the Jacobian matrix of system (10) at $(\frac{r_2}{a_2}, x_2^+)$, we have that the equilibrium is a linear center of system (10). And system (10) has a first integral

$$\frac{b_1}{a_1}(c_1 x_2^{a_1})^{\frac{1}{a_2}} + \frac{b_2}{a_2} x_2 + S - \frac{r_3}{a_1 a_2} \ln(c_1 x_2^{a_1}) - \frac{r_1}{a_1} \ln S = c, \quad c > 0.$$

Therefore the equilibrium $(\frac{r_2}{a_2}, x_2^+)$ is a center of system (10) and all the orbits of system (10) are closed orbits except this equilibrium on the foliation. Because c_1 is any positive constant, we obtain that all orbits of system (9) are closed orbits except \hat{E}_+ . Hence, the proof is finished. \square

Remark 16. When $\frac{r_1}{a_1} = \frac{r_2}{a_2}$ Theorem 15 shows that system (9) is completely integrable in $\text{Int}\mathbb{R}_+^3$. But it is not a bi-Hamiltonian system (see [21]).

The global dynamics of system (9) demonstrate that the principle of competitive exclusion holds for system (9) if and only if $\frac{r_1}{a_1} \neq \frac{r_2}{a_2}$. And the three species (two predators and a prey) will coexist in the form of periodic oscillation if $\frac{r_1}{a_1} = \frac{r_2}{a_2}$.

4. DISCUSSION

In this paper we completely analysis the global dynamics of the simplest two predators and a prey Lotka-Volterra model and find that the carrying capacity of the prey K and the ratio of the yield rate and the death rate for predators $\frac{r_i}{a_i}$, $i = 1, 2$ play important roles in the global dynamics of this model. This implies some interesting biology results. If the resource for prey is limited (i.e. K is bounded), then there are only three possibilities for two predators species and one prey species: either the principle of competitive exclusion holds, or the coexistence of three species in a stable steady state or the extinction of two predator species and the existence of prey. On the other hand, if the resource for prey is unlimited (i.e. K is unbounded), then there are only two possibilities for two predators species and one prey species: either the principle of competitive exclusion holds, or the coexistence of three species in periodic oscillations. These results lead to a new insight into the mechanism of natural selection and provide a new approach to the problem of biological pest control. Usually biological pest control requires the introduction of a harmless or less harmful predator decreasing the pest predator population to an acceptable level or completely annihilated the pest predator population, which implies the introduced predator species must have a higher survival capacity than the pest predator has in our imagination. Our results show that the intuition is true if the resource for prey is unlimited, and the intuition is not always true if the resource for prey is limited because the two predator species can eventually become extinct and only prey species survives (see statement (ii) of Theorem 7). Hence, this makes sense biologically in pest control.

It is worth to mention that the analysis method in this paper can be applied to m predators and n prey Lotka-Volterra model though our analysis uses the simplest two predators and a prey Lotka-Volterra model. The global dynamics of the m predator and n prey Lotka-Volterra model leaves to be revealed in future.

ACKNOWLEDGMENTS

The first author has been supported by the grants MINECO/FEDER MTM 2009-03437, CIRIT 2009SGR, FP7-PEOPLE-2012-IRSES 316338 and 318999, and ICREA Academia. The second author has been partially supported by the National Natural Science Foundations of China (No.10831003 & No.10925102) and the Program of Shanghai Subject Chief Scientists (No.10XD1406200).

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